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A Reassessment of the Genus *Ctenoblepharis* (Reptilia, Sauria, Iguanidae) with a Description of a New Subspecies of *Liolaemus multimaculatus* from Western Argentina

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ABSTRACT—A reassessment of the heterogeneous genus *Ctenoblepharis auctorum* is proposed, including the species *adpersus*, *stolzmanni*, *reichei* and probably *nigriceps*. *Phrynosaura* Werner, 1907, and *Helocephalus* Philippi, 1860, are synonyms of *Ctenoblepharis* Tschudi, 1845; *Ctenoblepharis anomalus*, *C. donosobarrosi*, *C. marmorata*, *C. schmidtii* and *C. jamesi* are evolutionary lines of the polymorphic genus *Liolaemus*. A distinct psammophilous species group is made up by *Liolaemus rabinoi* (Cei), *Liolaemus multimaculatus multimaculatus* (Duméril and Bibron) and *Liolaemus multimaculatus riojanus* subsp. nov. here described. Should these lizards be accorded a formal recognition, the generic name *Ortholaemus*, formerly used by Girard (1857), is available. A brief discussion of the disjunct distribution of the *rabinoi-multimaculatus* complex is presented.

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INTRODUCTION

The genus *Ctenoblepharis* was described by Tschudi (1845) for *C. adpersus*, a psammophilous species of tropidurine iguanid lizard from the coastal desert of Peru. Subsequently several additional species have been described in this genus, and still others that were initially placed in *Liolaemus*, *Helocephalus*, and *Phrynosaura* were later transferred to *Ctenoblepharis*. All of these forms exhibit a spectrum of common structural characteristics that are apparently adaptive to live in an arid, sandy environment; however, it now appears that several unrelated, geographically non-contiguous groups of species are involved. In the present work the genus *Ctenoblepharis* is redefined and restricted to *C. adpersus* and its close allies in the arid regions of northern Chile and Peru, and the remaining forms are reallocated to *Liolaemus*. In addition, two species from the deserts of central and coastal Argentina, *multimaculatus* and *rabinoi*, are accorded diverging position within *Liolaemus*, and a new subspecies of *multimaculatus* is described.

The Genus *Ctenoblepharis*

Subsequent to the description of *Ctenoblepharis adpersus* (Tschudi, 1845) from the arid coast of central Peru, five other species were described in this genus: *C. stolzmanni* (Steindachner, 1891) from the high cordillera of southern Peru and northern Chile, *C. jamesi* (Boulenger, 1891) from the high Andes of Tarapacá, Chile, *C. schmidtii* (Marx, 1960) known only from the type-locality in Antofagasta province, Chile, *C. donosobarrosi* (Cei, 1974) from southern Mendoza and northern Rio Negro provinces in western central Argentina, and *C. rabinoi* (Cei, 1974) known from the type-locality near Nihuil Dam, Mendoza province, Argentina. Donoso Barros (1958, 1971, 1972) further enlarged the genus by the transfer of several other forms initially described in other genera: *Liolaemus anomalus* (Koslow, 1895) from La Rioja province, Argentina; *Helocephalus nigriceps* (Philippi, 1860) from the Atacama desert of Chile; *Phrynosaura marmorata* (Burmeister, 1861) from the desert areas of Catamarca province, Argentina; *Phrynosaura reichei* (Werner, 1907) from the desert of Tarapacá in northern Chile; and *Phrynosaura werneri* (Müller, 1928) in western central

Argentina. Except for the synonymy of *Phrynosaura wernerii* with *Liolaemus anomalus* (Cei, in press), all of these species are currently considered valid species of *Ctenoblepharis*.

In his description of *Ctenoblepharis adspersus*, the generic type, Tschudi (1945) emphasized its very short, heavy, subtriangular head, granular scales on the upper eyelids, tubercular head scales with a moderately large interparietal scale, projecting palpebral fringes, distinct gular and antehumeral folds, smooth dorsal and ventral scales (the dorsals juxtaposed), tail length equal to the snout-vent length, and the presence of pterygoid teeth. This combination of character-states together with the presence of tricuspid marginal teeth was used by Donoso Barros (1971, 1972, pers. comm.) to distinguish *Ctenoblepharis* from other tropidurine iguanids such as *Liolaemus* and *Tropidurus*, and also to substantiate the synonymy of *Helocephalus* and *Phrynosaura* with *Ctenoblepharis*. Not all of these characters, however, are unique to the species allocated to *Ctenoblepharis* by Donoso Barros. For example, pterygoid teeth, tricuspid marginal teeth, a short tail, smooth juxtaposed dorsal and smooth ventral scales are found as well in some species of *Liolaemus* and in other tropidurine genera. Nevertheless four of these character-states do appear to be restricted to *adspersus* and several closely related and geographically approximate species (*stolzmanni*, *reichei*, *nigriceps*). These are: the peculiar subtriangular head shape; the granular or poorly differentiated smooth scales on the upper eyelid, with projecting superciliaries; the very prominent, comb-like palpebral fringes; and the deep transverse (not longitudinal) antehumeral and

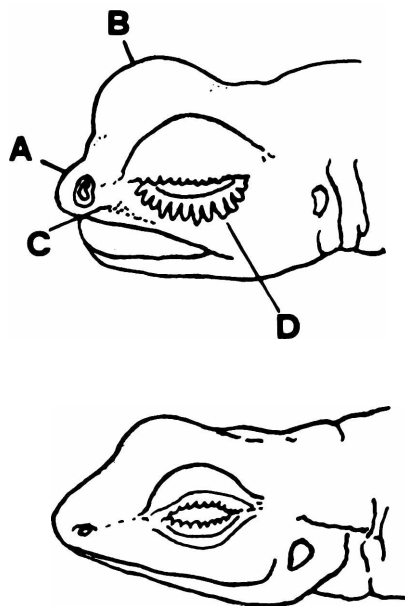


FIGURE 1. Top—Character states of *Ctenoblepharis*: A—pug-nosed snout and short triangular head; B—projecting ocular region; C—depressed loreal region; D—comb-like palpebral fringes.

Bottom—A comparative view of the head of *Liolaemus*.

neck folds, present in *adspersus* and *reichei* as a distinct gular fold. Additional details of head morphology are also shared by *adspersus*, *stolzmanni*, *reichei* and *nigriceps*: exceptional shortening of the snout, with prominent globous cheeks and a strikingly projecting ocular region; distance from anterior corner of eye to tip of snout noticeably less than diameter of eye; and, loreal region strongly depressed or concave above supralabials. These features of the head morphology are not shared with the remaining forms allocated to *Ctenoblepharis*, nor are they found in *Liolaemus* species or other tropidurine iguanids (Fig. 1).

An analysis of the remaining characters used by Tschudi and Donoso Barros to diagnose *Ctenoblepharis* presents a more complex picture. Smooth, juxtaposed body scales are present in *adspersus* and *nigriceps*; they are smooth but mostly subimbricate in *stolzmanni*, *reichei*, *schmidtii*, and *anomalus*; subimbricate or juxtaposed scales occur in *rabinoi*; weakly keeled subimbricate scales are present in *jamesi*, *donosobarrosi* and *Liolaemus multimaculatus*; and smooth but subimbricate scales have been reported for the poorly known species *marmorata* (citation). Smooth or faintly carinate, almost juxtaposed dorsal body scales are also present in some Andean species of *Liolaemus*: *multiformis*, *signifer*, *ruibali* and *duellmani*. The relatively short tail is also inadequate to diagnose *Ctenoblepharis* as defined by Donoso Barros. The tail length is about equal to the body length in *adspersus*, *stolzmanni*, *reichei*, *nigriceps*, *rabinoi*, *multimaculatus* and *anomalus*, but the

tail is longer in *jamesi*, *donosobarrosi*, *schmidtii*, and apparently in *marmorata*. Furthermore within the genus *Liolaemus* there are both long-tailed species groups (*elongatus* group *fitzingeri* group) as well as short-tailed groups (*magellanicus* group, *kingi* group). The interparietal scale is moderately large not only in all of the species mentioned, but also in most species of *Liolaemus*. Tricuspid marginal teeth are also present in most *Liolaemus* as well as in almost all other tropidurines, and pterygoid teeth are also present in some species of *Liolaemus* and in many other tropidurine iguanids (Etheridge, 1966).

It would appear from these studies that the species *adspersus*, *stolzmanni*, *reichei* and *nigriceps* form a rather homogeneous group of pug-nosed, fossorial, psammophilous lizards living in sandy environments from coastal Peru southward to the Atacama plateau of northern Chile. The remaining species placed in *Ctenoblepharis* by Donoso Barros appear to fall into three additional groups: *schmidtii* and *jamesi* from northern Chile; *anomalus*, *marmorata* and *donosobarrosi* of western Argentina; and *rabinoi* from central Argentina. As will be discussed below, *Liolaemus multimaculatus*, a form not referred to *Ctenoblepharis*, is quite close to *rabinoi*, and may be considered another member of this group. Although both *schmidtii* and *jamesi* were originally described as species of *Ctenoblepharis* they are in fact morphologically quite similar to the soft-scaled Andean species of *Liolaemus*, as for example *multiformis*, *signifer*, *ruibali* and *duellmani*. Characteristics of the *anomalus* group of western Argentina are: a broad, stout and compressed head with a concave loreal region, preanal pores in both males and females, a faint gular fold, a short tail with autotomy limited or absent, smooth subimbricate or juxtaposed dorsal body scales, a characteristic color pattern, and a very aggressive behavior. This species group has been the subject of a separate work (Ceí, in press) and will not be discussed in detail here.

The species *rabinoi* and *multimaculatus* appear to represent a very specialized group of psammophilous lizards restricted to bare dunes of the desert landscape in central and coastal Argentina, where they are highly fossorial, living under the sand during the very hot weather of the summer. In general aspect they are slender, with a non-autotomic tail equal to their head-body length. The head is depressed and elongate with a somewhat flattened, protruding jaw having a peculiar keel along each side formed by the lower edge of the infralabials. This keel is not unlike the maxillary keel found in the sceloporine iguanid genus *Uma* of the deserts of southwestern North America, and may serve the same function in burrowing (Fig. 2). Comb-like palpebral fringes are present above the eye as in *Ctenoblepharis* and also *Uma*, and the digits are fringed to a lesser extent than in *Uma*. In addition the nostrils open dorsally and are provided with a protective valvule. While some of their specializations are found as well in *adspersus* and its allies their differ in having a larger snout region, the ocular region is not especially prominent, the loreal region is not concave or depressed, the palpebral fringes are not as well developed, and both transverse as well longitudinal neck folds are present.

In conclusion, it would now appear that from within the enormously diverse and complex genus *Liolaemus* several different phyletic lines have independently acquired a number of morphological specializations that are adaptive for a fossorial, psammophilous life style. The recognition of any of these lines as a formal, supraspecific taxon would be difficult to justify at present. However, if *Ctenoblepharis* is recognized as a valid genus it should be restricted to the species *adspersus*, *stolzmanni*, *reichei*, and *nigriceps*. Should *multimaculatus* and *rabinoi* be accorded special, formal recognition, the subgeneric name *Ortholaemus* (Girard, 1857; type species *Ortholaemus beaglii* = *Liolaemus multimaculatus*) is available.

Liolaemus multimaculatus riojanus subsp. nov.

Holotype.—MF-21796, male collected Baldecitos, La Rioja province, western Argentina, on 11 February 1977, by J. M. Ceí and A. Lattuada.

Paratypes.—MF-21791-21795, 2 males, 2 females, 1 juvenile, with the same locality and data as the holotype; MF-21797-21800, 4 females, 10-12 km north Bermejo, San Juan province, western

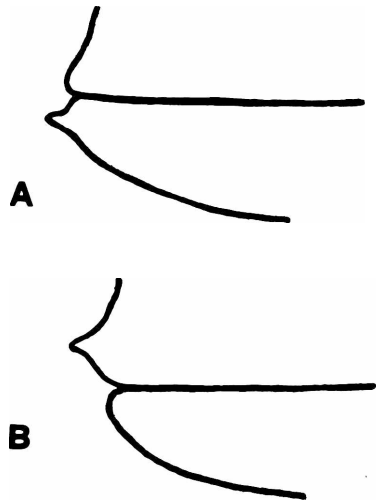


FIGURE 2. A—keeled jaw of *Liolaemus multimaculatus* and *Liolaemus rabinoi*; B—keeled maxillary of *Uma*.

Argentina, collected February 12, 1977, by J. M. Ceí and A. Lattuada; DC-JMC-1-2, 1 male, 1 female, with the same locality and data as the holotype; IBA-UNC-1238, 2 males, 3 females, 4 juveniles collected between Baldecitos and Pagancillos, La Rioja province, on November 13, 1976, by J. M. Ceí, and L. P. Castro. (Museum acronyms: MF = Museo Zoologico, Università di Firenze, Italy; DC-JMC = Diagnostic Collection J. M. Ceí; IBA-UNC = Instituto Biología Animal, Universidad Nacional de Cuyo, Mendoza, Argentina).

Diagnosis.—A subspecies of *Liolaemus multimaculatus* characterized by slender, smaller body, large lozenge-shaped dorsal scales and vertebral scales almost indistinguishable from dorsolaterals. Ground color reddish, scattered with brownish or brick red small spots.

Description of holotype.—Head wedge-shaped, flattened and elongate, less than one fourth of the body length. Transverse latero-gular and antehumeral folds; a Y-shaped longitudinal fold behind ear opening. No inferior gular fold; 6-7 transverse scale rows of closely imbricate, distally raised and acuminate scales in posterior gular region. Snout distinctly pointed; slightly protruding jaw, shoving a sharpened keel along each side, formed by the lower edges of infralabials. Neck narrower than head; cheeks slightly prominent. Head scales poorly differentiated. Rostral subtriangular and broad, limited by four small scales; frontals and frontoparietals very irregular; parietals and interparietal of about same size. Two interorbital scale rows; ten irregular supraoculars on each side. Subocular enlarged, separated from supralabials by 2-3 scale rows; eleven supralabials, nine infralabials. Temporal scales irregular, smooth and enlarged. Palpebral fringes developed; ear opening moderate, vertically extended, anteriorly bordered by larger granules. Nostrils opening dorsally, nasal valvule present. Neck and sides of neck granular. Dorsal scales lozenge-shaped, keeled, subimbricate, half size of ventrals. Lateral scales smaller than dorsal, almost granular; ventral scales quadrangular, smooth, imbricate. Caudal scales dorsally enlarged, trapezoidal, weakly carinate at base of tail, elsewhere keeled; limb scales enlarged, carinate, sharply pointed on external side, ventrally smooth, granular on posterior surface of thighs. Femoral patch present; toes fringed. Scales around midbody 75; ten preanal pores; 22-23 unkeeled lamellae under fourth toe. Length of head equal to length of 25 middorsal scales. Non-autotomic tail, same length as head-body.

Ground color reddish buff, with irregular transverse brownish or brick red spots, light-bordered behind; lateral blue spots involving 2-4 scales; head and limbs mottled with brownish and reddish spots. Ventral surface white, speckled with round black spots, paler on sides. Ventral surface of tail and limbs immaculate.

Measurements of the holotype in millimeters: total length 130, snout-vent 61.5, tail 72, axilla-groin 28, head length 14.5, head width 12.5, forelimb 22, hind limb 36.

Variation in the paratypes.—Female paratypes similar to the males in size, proportions and dorsal coloration, showing scanty lateral blue dots and lacking black round spots on the belly. Individual variation in head lepidosis remarkable; a distinct dark posthumeral spot present in the Bermejo population. Spotted venter and white preanal pores recognizable in juvenile male specimens (snout-vent 36 mm).

Measurements (in mm) based on 5 adult males and 10 adult females: total length: males 85-111, females 91-115; snout-vent length: males 45.5-54, females 43-56; tail: males 43-60, females 46-64; axilla-groin: males 20-24, females 20-27; head length: males 11.5-13.5, females 11-13.5; head width: males 9-11.5, females 8.5-11.5; forelimbs: males 17-21.5, females 16-22; hind limb: males 27-32.5, females 25-32.5.

Distribution.—From Pagancillo sand flats, La Rioja province, to bare dunes near Caucete and Encon, San Juan province (western Argentina).

Etymology.—The subspecific name denotes the geographical area where this form was discovered.

Remarks on the *multimaculatus* Group

Several characteristics support the proposed subspecific status of *multimaculatus riojanus*. The eastern nominal form differs from *riojanus* by larger body; keeled, almost rhomboidal dorsal scales,

slightly smaller than the western form; vertebral scales somewhat smaller than dorsolaterals and distinctly keeled; small lateral scales, almost granular, yet faintly keeled close to the ventral scales; ventral scales about four times as large as laterodorsals; ochre-brownish ground color on the dorsum, with scattered, very distinct dark brown spots; round blue dots between axilla and groin involving a single scale, rarely 2-3. On the contrary both geographical forms can be easily differentiated from the allopatric *Liolaemus rabinoi* (Ceï, Lanza and Poggesi, 1976). *Liolaemus rabinoi* is a smaller and slender species, showing evident prognathism, slightly carinate, frequently juxtaposed scales on the back, high number of scales around midbody and a very characteristic bluish gray dorsal coloration, with evident lateral blue spots involving up to 15-18 scales in the males. It lacks closely imbricate and acuminate, distally raised, transverse scale rows in the posterior gular region. That character is developed in the adult specimens of *multimaculatus multimaculatus* and *multimaculatus riojanus*.

The disjunct ranges of closely related forms such as *multimaculatus multimaculatus* and *multimaculatus riojanus* suggest a former continuous distribution. Their psammophilous trends make them significant members of the desert communities. The coastal sand-banks of the Atlantic shores, between Mar de Ajó and San Blas Bay, and the bare dunes extending from La Rioja mountains to San Juan River southward, are at present separated by more humid areas. However, during the last glaciation, they were extensively connected by wide-spread loess and eolian deposits (Fig. 3). That xeric formation, named "Medano Invasor" by some Argentine geologists (Groeber, 1936; Tapia, 1935, 1937; Zetti, 1964), was tentatively referred to the upper sediments covering the fluvio-lacustrine deposits of interglacial beds (Riss/Würm), from about 30,000-25,000 to 10,000 years ago. The recent evolutionary history of the *multimaculatus* group probably underwent the holocene paleoclimatic events and the increasing environmental humidity following the last glacial retreat. The discontinuous distribution of the *multimaculatus-rabinoi* complex can be explained by the disappearance of interposed quaternary loess and eolian deposits. The analogy with the disjunct ranges of *Liolaemus occipitalis* and *Liolaemus lutzae* from the sandy coastal region of southeastern Brazil is remarkable (Vanzolini and Ab'Saber, 1968).

Liolaemus rabinoi is only known for the bare dunes, scattered with *Juncus* and *Atriplex*, along the artificial Nihuil Lake, a broad flat basin formed by the Atuel River (35° south lat., 69° west long.). Prior to Nihuil dam construction, in 1936, all this region was a wide, isolated marshy or sandy depression, where *Liolaemus rabinoi* was probably endemic. The morphological differentiation of this species suggests a longer period of geographical isolation in comparison of the shorter disjunction of *multimaculatus multimaculatus* and *multimaculatus riojanus*.

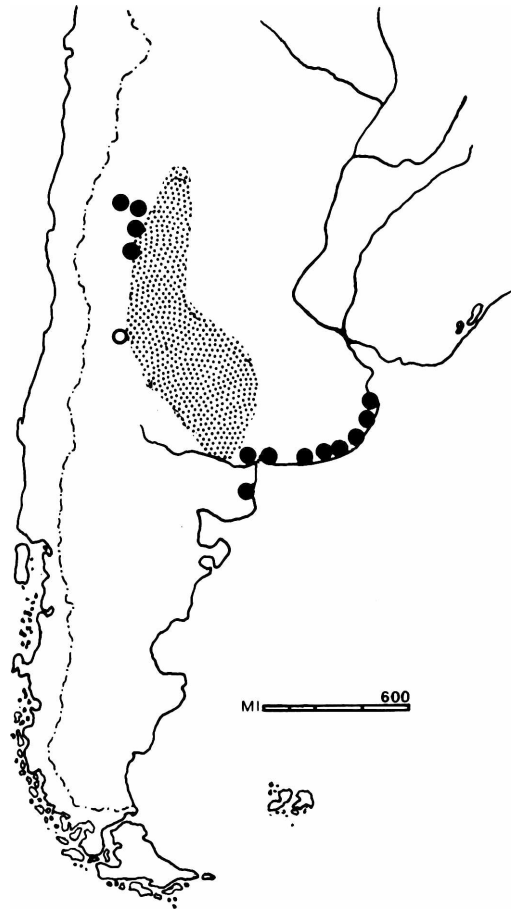


FIGURE 3. Dotted area: the Upper Pleistocene "Medano Invasor" Formation. Black circles: reported localities of *Liolaemus multimaculatus*. Open circle: endemic area of *Liolaemus rabinoi*.

Liolaemus darwini, *Liolaemus gracilis* and *Cnemidophorus longicaudus* belong to the saurian community living in the sandy environment of *Liolaemus rabinoi*. *Liolaemus anomalus* and an undescribed form of the *fitzingeri* group are found in the reddish bare dunes inhabited by *multimaculatus riojanus*. *Liolaemus darwini* from La Rioja flats shows a peculiar red morph, being homochromic and strikingly similar to sympatric individuals of *multimaculatus riojanus*. *Liolaemus multimaculatus multimaculatus* is the predominant tropidurine lizard in coastal sand-banks of the Buenos Aires province. *Liolaemus wiegmanni*, *Liolaemus gracilis* and *Proctotretus pectinatus* were reported for the bushy neighboring areas bordering the Atlantic shores (Gallardo, 1966).

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